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Comparison of Foraging Performance of Diploid and Triploid Saugeyes (Sauger × Walleye)

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Abstract.—To evaluate the performance and quality of triploid saugeyes (female walleye *Stizostedion vitreum* × male sauger *S. canadense*), we compared their foraging behavior with that of diploid conspecifics. Triploidy was induced by heat-shocking fertilized eggs for 15 min at 31°C 5 min after fertilization, and ploidy was evaluated by flow cytometry. In three experiments using both ploidy groups we evaluated (1) prey selection with respect to fathead minnow *Pimephales promelas* and the daphnia *Daphnia pulex*; (2) aggression and food consumption by individual saugeye predators during a single feeding session; and (3) handling time of a single large (50–60% of predator body length) minnow. Juvenile diploid saugeyes foraged more successfully than triploid conspecifics. Diploids caught fathead minnow significantly more frequently than did triploid fish (59% and 39% of available minnow, respectively) while consuming significantly fewer daphnids. Triploids fed on zooplankton to a larger extent. Experiment 2 revealed that diploid and triploid fish did not differ in the number of prey captured up to the satiation level. However, the number of attempted attacks (20.2 ± 5.8 [mean ± SD] versus 29.3 ± 7.3 per predator per feeding session) and the percentage of unsuccessful ones (48 ± 13.5% versus 62.3 ± 9.4%) were always higher in triploids. As a consequence, the time needed to reach satiation was also longer for triploids. Diploid saugeyes had to make significantly fewer attacks for a successful catch and needed less time to handle the prey once it was captured. Thus, triploid juvenile saugeyes exhibited less efficient foraging than did diploids, which could reduce the former's growth, increase their risk of predation, and decrease their survival after stocking.

Manipulation of ploidy in fish has become a viable tool in aquaculture and fisheries management (Gervai et al. 1980; Thorgaard et al. 1992). Inland reservoirs in Ohio are stocked with juvenile, pond-raised saugeyes (hybrids of female walleyes *Stizostedion vitreum* and male saugers *S. canadense*). Recent concerns regarding the routine release of fertile hybrid fish (Rahel 2000) and a realistic threat to the genetic integrity of parental species in the wild (Templeton 1987; Philipp et al. 1993; Corley-Smith and Brandhorst 1999) dictated a need for alternative stocking strategies. The production of triploid saugeyes would provide two advantages to fish management over the traditional diploid fish: (1) because triploids are sterile, the genetic integrity of parental species would be preserved (Billington et al. 1997) and (2) triploids have the potential for faster growth (Habicht et al. 1994; Bonnet et al. 1999; Felip et al. 1999). Thus, stocking triploids could provide viable sport fisheries while protecting wild populations from introduced fertile hybrids.

The extra set of chromosomes in triploid fish, however, can alter an organism's behavior and physiological functions (Aliah et al. 1990), which in turn can affect growth and survival, thereby compromising overall performance. Comparative studies of the growth performance of triploid and diploid taxa have been contradictory and inconsistent across different species. Most studies have failed to clearly demonstrate the growth advantages of triploids over diploids (Myers and Hershberger 1991; Parsons 1993; Habicht et al. 1994; Bonnet et al. 1999; Felip et al. 1999). In fact, the expected growth advantage of triploids appeared only in a few studies (Bramick et al. 1995; Qin et al. 1998). Interestingly, several authors have demonstrated that diploids outperformed triploids in

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survival and growth (Wolters et al. 1991; Mckay et al. 1992; Carter et al. 1994; Ojolick et al. 1995).

Behavioral impairments caused by an extra set of chromosomes are possible but are seldom cited as an alternative explanation for the lower performance of triploid fish. Triploid salmonids cultured with diploids grew more slowly than those raised alone (Galbreath et al. 1994). Interestingly, in all the studies of competitive behavior with respect to ploidy type the fish were fed formulated diets. Under these circumstances, only competition among foraging fish was evaluated; interactions between predator and prey and the consequences of these interactions for growth and survival were not considered.

This study evaluates selected elements of juvenile diploid and triploid saugeye feeding behavior on natural prey. We compare prey selection patterns, ingestion rates, and the handling time of a large prey between diploids and triploids. Potential differences in feeding behavior and foraging success could be useful in projecting the performance of these fish in the wild.

Methods

Triploid saugeyes were produced according to the procedure of Garcia-Abiado et al. (1999). On April 2, 1998, walleye eggs were stripped from 16 ovulated females caught from C. J. Brown Reservoir, Ohio, and fertilized with fresh sauger sperm from 4 males collected from the Ohio River. Fertilization procedures followed that described by Czesny and Dabrowski (1998). Fertilized eggs were heat-shocked at 31.0 ± 0.1°C for 15 min starting 5 min after fertilization. Heat-shocked eggs were transported (45 min) in 8°C water to Hebron State Fish Hatchery, Hebron, Ohio, for incubation. The triploidy (3n) induction rate of saugeye eggs at the eyed stage was determined by flow cytometry following Lin and Dabrowski (1996); diploid (2n) saugeyes were produced using gametes from these same adult fish.

On April 16, 1998, newly hatched swim-up diploid and triploid larvae were stocked into separate ponds at 395,000 fish/ha. These ponds were fertilized weekly according to Culver (1996). Water temperature (18.2 ± 3.6°C), dissolved oxygen (11.1 ± 3.6 mg/L), and Secchi depth (0.7 ± 0.2 m) were considered normal during the 40 d of rearing. On May 5, 1998, ponds were seined. About 500 diploids and 1,000 triploids were transported to the Ohio State University Research and Extension Center in Piketon, Ohio, and maintained indoors in two circular 800-L tanks with a flow rate of 5 L/min. After 2 d of acclimation, fish were segregated into several size groups and placed in smaller (50-L) circular tanks to avoid cannibalism. The flow rate was 0.5 L/min, the photoperiod was set at 15 h light: 9 h dark, and light during the daylight hours was dim (80 lx). Water temperature and oxygen concentrations were stable at 20°C and 8 mg/L, respectively. Fish were fed fathead minnow *Pimephales promelas* twice a day. Both ploidy groups were starved for 24 h prior to each experiment.

The prey preference and foraging efficiency of diploid and triploid saugeye juveniles were compared in experiment 1. The mean (±SD) length of 2n ($N = 9$) and 3n ($N = 12$) fish was 43.8 ± 0.8 and 42.8 ± 1.2 mm, respectively. Individuals from both groups were placed in 40-L round tanks (one per tank). After 2 h of acclimation, the daphnia *Daphnia pulex* were added to each tank, either alone at a density of 10/L or along with three fathead minnow (mean length, 19.1 ± 1.5 mm; $N = 30$). Since zooplankton size can affect foraging success (if predation is size selective), only daphnia that passed through a 1-mm sieve (mesh size) but not through a 0.75-mm sieve were used. The average length of the daphnids used in the experiment was 1.8 ± 0.2 mm ($N = 30$). Measurements were taken from the furthest projection of the head to the point of insertion of the caudal spine (Lawrence et al. 1987). Saugeyes were allowed to forage for 15 min, after which each was removed and placed in an individual plastic container filled with ice-cold water. When the fish were anesthetized, blood was sampled from each individual saugeye from the 3n group for ploidy verification (fish from the 2n group were assumed to be diploid) by cutting the caudal fin off and collecting one drop of blood from the caudal vein in individual Eppendorf tubes filled with 5% buffered dimethyl sulfoxide solution. Fish were fixed in 10% formaldehyde solution for stomach content analysis; upon dissection, daphnia and fathead minnow were counted. The ploidy of 3n saugeyes was determined by flow cytometry following techniques described by Lin and Dabrowski (1996).

In experiment 2, we compared the consumption rates of diploid and triploid saugeye juveniles. The mean (±SD) length of 2n ($N = 12$) and 3n ($N = 8$) fish was 55.8 ± 1.5 and 55.0 ± 2.0 mm, respectively. Individual saugeyes from the 2n and 3n groups were placed in 30-L aquaria (one per aquarium). After 3 h, each fish was offered 15 fathead minnow (mean length, 17.7 ± 1.3 mm; $N = 30$) and allowed to forage for 30 min, during which we

counted the total number of attacks and the number of successful ones and measured the time required by each predator to reach satiation. Satiation was assumed when fish ceased foraging behavior and remained inactive throughout the remainder of the experimental session. Based on these data, capture efficiency (number of prey eaten/number of total attacks) was calculated. After 30 min, saugeyes were removed from the aquaria and the remaining minnow were counted. Blood sampling for ploidy verification and the preservation of the fish were as described for experiment 1.

In experiment 3, we compared the capture efficiency and handling time of a single large prey by 2n and 3n saugeye juveniles. The mean (±SD) length of 2n (N = 20) and 3n (N = 7) fish was 45.5 ± 0.8 and 45.9 ± 0.7 mm, respectively. Individual fish were placed in 30-L aquaria; after 3 h, each was exposed to a single fathead minnow (mean length, 24.7 ± 0.5 mm; N = 30) for 10 min. We recorded the number of attempted attacks prior to the successful one and the time required by each predator to ingest captured prey (handling time). Blood was sampled for ploidy verification in 3n saugeyes as previously described.

The mean values of all measured variables in each experiment were compared using the t-test (SPSS 1995). Percentage data were arcsine transformed. Normality and homogeneity of variance were confirmed for all data before statistical analysis. The rejection level for all statistical analyses was set at $\alpha = 0.05$.

Results

Prey Preference and Foraging Efficiency (Experiment 1)

When daphnia alone were offered to juvenile saugeyes, the number consumed per fish was not significantly different (F = 0.009; df = 5; P = 0.9) between diploids (41.7 ± 17.6 per fish; N = 3) and triploids (40.7 ± 3.1 per fish; N = 3). However, when three fathead minnow were available as alternative prey, diploids consumed significantly (F = 16.75; df = 20; P = 0.0006) fewer daphnia (0.4 ± 0.3 per fish; N = 12) than did triploids (9.6 ± 4.7 per fish; N = 9). Moreover, when both prey were available, diploids consumed a significantly (F = 5.78; df = 20; P = 0.03) higher proportion of minnow than did their triploid conspecifics (0.7 ± 0.2 versus 0.4 ± 0.1).

Measures of Feeding Aggressiveness (Experiment 2)

Diploid and triploid juvenile saugeyes captured on average the same number of prey (F = 1.09; df = 19; P = 0.3) during their foraging sessions when offered 15 fathead minnow (Figure 1A). However, diploid saugeyes made fewer attacks than triploid conspecifics (F = 17.20; df = 19; P = 0.0006) to obtain the same foraging yield (Figure 1B). Thus, diploids had higher capture efficiency than triploids (F = 11.4; df = 19; P = 0.003; Figure 1C). Consequently, diploids reached satiation and ended foraging twice as fast as triploids (F = 64.4; df = 19; $P < 0.0001$; Figure 1D).

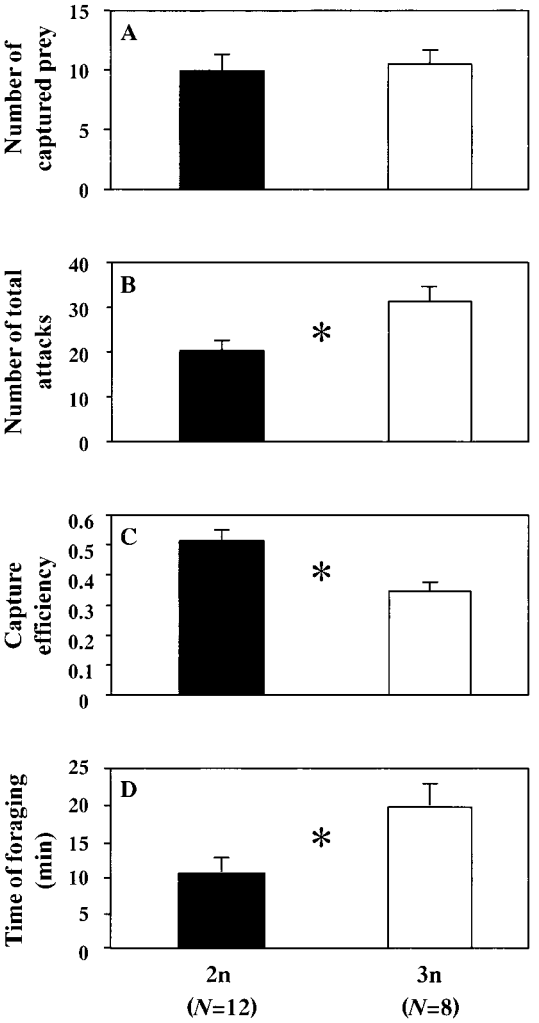

FIGURE 1.—**(A)** Average number of captured prey, **(B)** number of total attacks, **(C)** capture efficiency, and **(D)** time of foraging of diploid (2n; black bars) versus triploid (3n; white bars) saugeyes in experiment 2. Asterisks indicate significant ($P < 0.05$) differences between ploidy groups.

Ability to Handle Large Prey (Experiment 3)

When saugeyes were faced with a single large fathead minnow, the diploids made significantly ($F = 6.13$; df = 26; $P = 0.02$) fewer attacks (1.6 ± 0.3; $N = 20$) prior to the successful one than did the triploids (3.4 ± 1.2; $N = 7$). Moreover, diploids required less ($F = 5.97$; df = 26; $P = 0.03$) time than did triploids to ingest captured prey (36.5 ± 4.2 s versus 48.9 ± 10.3 s).

Discussion

Behavioral comparisons between diploid and triploid fish are limited to analyses of the interactions between different ploidy groups reared together and the effect of these interactions on hierarchy structure (O'Keefe and Benfey 1997), variation in food intake (Carter et al. 1994), and consequently growth of the fish (see review by Benfey 1999). For example, triploid Atlantic salmon *Salmo salar* grew faster than diploid conspecifics when reared separately (Galbreath et al. 1994). However, when pooled and raised until after smoltification, diploids outperformed triploids and grew faster. Several studies attributed similar results to the reduced aggressiveness of triploid fish compared with diploid conspecifics (Cassani and Caton 1986; Tave 1993). Scientists are uncertain whether this is associated with alterations in the central nervous system or reduced production of the androgens that promote aggressive behavior (Benfey 1999).

We have demonstrated that the foraging behavior of juvenile triploid saugeyes differs from that of diploids in laboratory tanks; if this difference occurs in nature, it may contribute to differential survival. Diploids captured more minnow than triploids and almost totally neglected daphnia, whereas triploids foraged more frequently on daphnia. Diploid saugeyes tended to select larger prey than triploid conspecifics. Cladocerans of the size we used provided less reward per effort than the nearly 20-mm fathead minnow. The differences with respect to prey selection that we observed in experiment 1 can lead to a discrepancy in growth rates between different ploidy groups if such a selection pattern is consistent. The switch to piscivory is a naturally occurring step in the life history of many juvenile percid fishes (Stahl and Stein 1994), providing a substantial energetic advantage over foraging on small prey. Thus, diploid saugeyes, which selected minnow more often in experiment 1, appear to exhibit the switch to piscivory earlier in their ontogeny then triploid conspecifics. Consumption of big prey may lead to a faster growth rate, allowing fish to escape the ''predation gape'' faster (Houde 1987) and substantially increasing the probability of survival (Bailey and Houde 1989).

Previous studies of differential growth between ploidy groups used formulated diets to feed the experimental animals. However, this approach does not consider the behavioral interactions between predators and prey that might strongly influence the success of the predators in reservoirs. Feeding on a formulated diet does not require the special foraging skills that are necessary for foraging in the wild, and this may explain the frequently reported lack of difference in growth between diploids and triploids under aquaculture conditions (Johnstone et al. 1991; Myers and Hershberger 1991; Galbreath et al. 1994). In trials with a single prey type (daphnia, experiment 1), diploids and triploids consumed the same number of prey. When foraging on relatively easy-to-capture prey such as daphnids, triploids perform comparably to diploids. Under natural conditions, however, predators must find, pursue, capture, and ingest their prey. The potentially inferior foraging skills of triploid fish may become apparent in reservoirs, leading to poor growth and perhaps lower survival.

The results of experiments 2 and 3 indirectly indicate that triploid saugeyes may face higher predation risk when foraging in the natural environment. Even though diploids and triploids reached satiation after ingesting the same number of minnow on average, capture efficiency was greater and the total time of foraging shorter for diploids. Diploids exhibited significantly greater capture efficiencies that translated into significantly shorter average foraging times. Extended foraging time in triploid fish would substantially increase their predation risk in a natural environment because fish are more susceptible to predators while foraging (Milinski 1984; Walters and Korman 1999). Therefore, the more efficient the predator and the shorter the foraging time, the lower the risk of being preyed upon (Szendrey and Wahl 1995). Similarly, longer handling times for large prey would also prolong triploids' exposure to potential predators and reduce their survival.

Diploid foraging behavior, which more closely approximates optimal foraging, ultimately will result in a higher growth rate. A greater body size at the end of the growing season should enhance the chance of overwinter survival (Copeland and Carline 1998) and, ultimately, recruitment.

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References

Aliah, R. S., K. Yamaoka, Y. Inada, and N. Taniguchi. 1990. Effects of triploidy on tissue structure of some organs in ayu. Nippon Suisan Gakkaishi 56: 569–575.

Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology 25:1–83.

Benfey, T. J. 1999. The physiology and behavior of triploid fishes. Reviews in Fisheries Science 7:39–67.

Billington, N., R. C. Brooks, and R. C. Heidinger. 1997. Frequency and natural hybridization between saugers and walleyes in the Peoria Pool of the Illinois River, as determined by morphological and electrophoretic criteria. North American Journal of Fisheries Management 17:220–224.

Bonnet, S., P. Haffray, J. M. Blanc, F. Vallee, C. Vauchez, A. Faure, and B. Fauconneau. 1999. Genetic variation in growth parameters until commercial size in diploid and triploid freshwater rainbow trout (*Oncorhynchus mykiss*) and seawater brown trout (*Salmo trutta*). Aquaculture 173:359–375.

Bramick, U., B. Puckhaber, H.-J. Langholz, and G. Horstgen-Schwark. 1995. Testing of triploid tilapia (*Oreochromis niloticus*) under tropical pond conditions. Aquaculture 137:343–353.

Carter, C. G., I. D. McCarthy, D. F. Houlihan, R. Johnstone, M. V. Walsingham, and A. I. Mitchell. 1994. Food consumption, feeding behaviour, and growth of diploid and triploid Atlantic salmon, *Salmo salar* L., parr. Canadian Journal of Zoology 72:609–617.

Cassani, J. R., and W. E. Caton. 1986. Growth comparisons of diploid and triploid grass carp under varying conditions. Progressive Fish-Culturist 48: 184–187.

Copeland, T., and R. F. Carline. 1998. Overwinter survival and lipid content of walleye fingerlings. North American Journal of Fisheries Management 18: 383–390.

Corley-Smith, G. E., and B. P. Brandhorst. 1999. Preservation of endangered species and populations: a role for genome banking, somatic cell cloning, and androgenesis. Molecular Reproduction and Development 53:363–367.

Culver, D. A. 1996. Fertilization procedures for pond culture of walleye and saugeye. Pages 115–122 *in* R. C. Summerfelt, editor. Walleye culture manual. North Central Regional Aquaculture Center (NCRAC), Iowa State University, NCRAC Culture Series 101R, Ames.

Czesny, S., and K. Dabrowski. 1998. The effect of egg fatty acid concentrations on embryo viability in wild and domesticated walleye (*Stizostedion vitreum*). Aquatic Living Resources 11:371–378.

Felip, A., S. Zanuy, M. Carrillo, and F. Piferrer. 1999. Growth and gonadal development in triploid sea bass (*Dicentrarchus labrax* L.) during the first two years of age. Aquaculture 173:389–399.

Galbreath, P. F., W. St. Jean, V. Anderson, and G. H. Thorsgaard. 1994. Freshwater performance of all-female diploid and triploid Atlantic salmon. Aquaculture 128:41–49.

Garcia-Abiado, M. A. R., K. Dabrowski, J. E. Christensen, S. Czesny, and P. Bajer. 1999. Use of erythrocyte measurements to identify triploid saugeyes. North American Journal of Aquaculture 61:319–325.

Gervai, J., S. Peter, A. Nagy, L. Horvath, and V. Csanyi. 1980. Induced triploidy in carp *Cyprinus carpio* L. Journal of Fish Biology 17:667–671.

Habicht, C., J. E. Seeb, R. B. Gates, I. R. Brock, and C. A. Olito. 1994. Triploid coho salmon outperform diploid and triploid hybrids between coho salmon and chinook salmon during their first year. Canadian Journal of Fisheries and Aquatic Sciences 51:31–37.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17–29 *in* R. D. Hoyt, editor. 10th annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.

Johnstone, R., H. A. McLay, and M. V. Walsingham. 1991. Production and performance of triploid Atlantic salmon in Scotland. Canadian Technical Report of Fisheries and Aquatic Sciences 1789:14–36.

Lawrence, S. G., D. F. Malley, W. J. Findlay, M. A. Maclver, and I. L. Delbaere. 1987. Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. Canadian Journal of Fisheries and Aquatic Sciences 4: 264–274.

Lin, F., and K. Dabrowski. 1996. Effects of sperm irradiation and heat shock on induction of gynogenesis in muskellunge (*Esox masquinongy*). Canadian Journal of Fisheries and Aquatic Sciences 53:2067–2075.

Mckay, L. R., P. E. Ihssen, and I. Mcmillan. 1992. Growth and mortality of diploid and triploid tiger trout (*Salmo trutta* × *Salvelinus fontinalis*). Aquaculture 106:239–251.

Milinski, M. 1984. A predator's costs of overcoming the confusion-effect of swarming prey. Animal Behaviour 32:1157–1162.

Myers, J. M., and W. K. Hershberger. 1991. Early growth and survival of heat-shocked and tetraploid-derived triploid rainbow trout *Oncorhynchus mykiss*. Aquaculture 96:97–108.

Ojolick, E. J., R. Cusack, T. J. Benfey, and S. R. Kerr. 1995. Survival and growth of all-female diploid and triploid rainbow trout (*Oncorhynchus mykiss*) reared

at chronic high temperature. Aquaculture 131:177–187.

O'Keefe, R. A., and T. J. Benfey. 1997. The feeding response of diploid and triploid Atlantic salmon and brook trout. Journal of Fish Biology 51:989–997.

Parsons, G. R. 1993. Comparisons of triploid and diploid white crappies. Transactions of the American Fisheries Society 122:237–243.

Philipp, D. M., J. M. Epifanio, and M. J. Jennings. 1993. Conservation genetics, and current stocking practices—are they compatible? Fisheries 18(12):14–16.

Qin, J. G., A. W. Fast, and H. Ako. 1998. Growth performance of diploid and triploid Chinese catfish (*Clarias fuscus*). Aquaculture 166:247–258.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288:854–856.

SPSS. 1995. SPSS 7.5 for Windows. SPSS, Inc., Chicago.

Stahl, T. P., and R. A. Stein. 1994. Influence of larval gizzard shad (*Dorosoma cepedianum*) density on piscivory and growth of young-of-year saugeye (*Stizostedion vitreum* × *S. canadense*). Canadian Journal of Fisheries and Aquatic Sciences 51:1993–2002.

Szendrey, T. A., and D. H. Wahl. 1995. Effect of feeding experience on growth, vulnerability to predation, and survival of esocids. North American Journal of Fisheries Management 15:610–620.

Tave, D. 1993. Growth of triploid and diploid bighead carp, *Hypophthalmichthys nobilis*. Journal of Applied Aquaculture 2:13–25.

Templeton, A. R. 1987. Coadaptation and outbreeding depression. Pages 105–116 *in* M. E. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusetts.

Thorgaard, G. H., P. D. Scheerer, and J. Zhang. 1992. Integration of chromosome set manipulation and transgenic technologies for fishes. Molecular Marine Biology and Biotechnology 1:251–256.

Walters, C., and J. Korman. 1999. Linking recruitment to trophic factors: revisiting the Beverton−Holt recruitment model from a life history and multispecies perspective. Reviews in Fish Biology and Fisheries 9:187–202.

Wolters, W. R., C. G. Lilyestrom, and R. J. Craig. 1991. Growth, yield, and dress-out percentage of diploid and triploid channel catfish in earthen ponds. Progressive Fish-Culturist 53:33–36.